CONTRIBUTIONS TO THE STUDY OF COLOUR MARKING AND OTHER VARIABLE CHARACTERS OF *ANOPHELINAE* WITH SPECIAL REFERENCE TO THE SYSTEMATIC AND PHYLOGENETIC GROUPING OF SPECIES

BY

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I. VARIATION IN COLOUR MARKING OF *ANOPHELINAE*

Nature of colour marking. With few exceptions, the markings of Anophelines are due to the varied distribution of light and dark scales. A mixture of light and dark scales may occur, e.g., on the wing veins of certain species or on the legs when these show mottling; but the most striking feature of the ornamentation of the sub-family is the occurrence of patches of either dark or light scales forming dark or light spots respectively. Where the dark scales predominate the appearance is that of light spots on a dark surface; where, on the other hand, the extent of light scaling is greater, an appearance of dark spots on a light ground is produced.

Leucogenetic centres and residual pigment areas. In a great many species the *scheme* of coloration is similar, the actual markings being brought about merely by different degrees of development of the scheme. The process of advancing ornamentation is one of increased whitening, and consists in the progressive appearance and spread of pale areas which have their origin at certain fixed points (leucogenetic centres).

Although the pale areas developing from these centres may spread until they coalesce with neighbouring pale areas, they do not, as a rule, do this, and there is a distinct hesitation shown at the final extinction of intervening dark areas. Also extension of the pale areas does not necessarily encroach equally on both sides of a dark area, and the behaviour of markings in this respect suggests that there exist something very like actual pigment centres having a definitely fixed position. Points at which the pigment seems thus to make a last stand will be referred to as *residual pigment areas*, or simply as pigment centres. In some cases centres become quite obliterated, some being apparently less resistant than others, but even in a high degree of whitening, such as frequently occurs in the case of the wing, where many of the pigment areas are displayed as mere points, the number actually present is not much reduced. A row of these pigment centres lying near the ends of the longitudinal veins of the wing constitute the marginal spots of Donitz, and others have an equally fixed and characteristic nature.

By referring markings to the leucogenetic centres which produce them (and so far as one can see, these centres of whitening are a very real phenomenon), and to the position of the pigment centres, the study of colour markings is greatly simplified.

Position of colour markings. The most important colour markings are those of the palps, legs and wings. There are, of course, variations in the coloration of other parts of the body which may assume importance in particular species.

Almost all Anophelines have a head covered with dark scales behind, and with a ' forehead ' patch of pale white or creamy scales prolonged forward as a tuft between the eyes. The *absence* of this marking would be an important feature in any species.

In the case of the proboscis, only a few species show any ornamentation other than the light tip due to the fact that the labellae are not dark scaled like the rest of the proboscis. But a very striking variation is seen in a few species where the outer portion of the proboscis is pale or snowy white.

Markings of the palps. A certain number of species show palps without any markings (unbanded palps). In some cases there is a faint indication of bands, due very often to the chitin showing at the joints, but there is no actual pale ornamentation. This is the condition which is sometimes referred to as palpal banding in *A. nigripes*, Staeger. *A. immaculatus*, Theo., also stated to have banded palps, shows very indefinite and indistinct ones, not at all sharply marked as in ordinary Anophelines.

Entirely unornamented palps are present in all *Stethomyias*, including *S. corethroides*, Theo. (vide section on scale structure), and *S. aitkeni*, James and Liston. Unbanded palps are also commonly present in *Anopheles*, and occur in *Myzorhynchus* and *Cycloleppteron*. Otherwise the palps are usually ornamented.

In *Anopheles* the unspotted wing species also have unbanded palps (except *A.* (?) *smithi*, Theo.*). The species *A. gigas*, Giles, and *A. simlensis*, James, with banded palps have been separated by James[1] as *Patagiamyia*. *A. formosus*, Ludlow, since it is a hill species whose description closely resembles that of *gigas*, would seem also to be a *Patagiamyia*. *A. punctipennis*, Say., which is a *Patagiamyia* (vide section on scale structure), has banded palps. It would be very interesting to know what was the condition of the prothoracic lobes in *A. eiseni*, *A. crucians*, etc. *A. welcomei*, Theo., is a peculiar species; it has no prothoracic tuft, but I am doubtful if it should be considered as an *Anopheles*.

When the palps are ornamented, this is in the form of bands, supplemented in some cases by extra spots of white (speckling) on certain segments.

It is usual to talk of four or three-banded palps, etc., some of the bands being described as broad or narrow, as the case may be. The only accurate method is to refer to the position of the bands in respect to the palpal segments. This relation is most easily expressed in terms of leucogenetic centres. In spite of considerable variety of appearance, a comparatively few general schemes of coloration associated with different relative lengths of the palpal

* Note.—This species has a scale tuft on the prothorax and is therefore not an Anopheles in the sense of James.

segments (vide section on structural variation) can be made to account for the markings.

SCHEME A. Palps with leucogenetic centres at each end of the segments, but none of these actively spreading.

The effect of the appearance of the leucogenetic areas (following upon complete absence of banding) in this scheme is the production of four narrow pale bands, including the pale apex. If the species be orthodactylous†, a somewhat different appearance is given to that produced in the case of a markedly heterodactylous* species (compare *C. pulcherrima* with the variety of *P. nursei* showing a dark apical band. Plate V, figs. 8 and 10).

This degree of extension of whitening is not exceeded in *Myzorhynchus*, and is typical of palpal ornamentation seen in *Myzorhynchus*, *Cycloleppteron*, *Arribalzagia*, *Patagiamyia* and *Cellia*.

It seems to be a stable condition, and is but little liable to variation in individuals belonging to these groups. In *Myzomyia*, *Pyretophorus* and *Nyssorhynchus* this stage is unusual, and when it does occur it is most often as an individual variation, e.g., the four-banded palp varieties of *N. fuliginosus*, *Ne. fowleri* and *P. nursei*. A permanent four-banded condition in this group is seen in *P. cinereus*, Theo.

SCHEME B. Leucogenetic centres at the ends of the segments, with that at the end of the apical segment active.

In this scheme the apical centre extends, making the apical segment entirely pale. This results in the ordinary type of three-banded palp. Considerable difference in general appearance again depends on whether the palp is orthodactylous or heterodactylous (Plate V, figs. 11-13).

The narrow apical band in *Myzomyia*† (*culicifacies*, *funestus*, etc.) is homologous in regard to extent of palp involved with the broad apical band of *Pm. rossi*, but not with the narrow apical band in *Pt. simlensis* or *C. pulcherrima*. The broad band in

* *Vide* Section III.

† NOTE.—As pointed out by Edwards[6], *Nyssorhynchus*, Blanchard (= *Laverania*, Theo.) having as type species *argyrotarsis*, Rob-Desv., must take precedence over *Cellia*, Theo., a new name being required for the group generally known as *Nyssorhynchus*. Again *rossi*, Giles, is the type species of *Myzomyia*, Blanchard (= *Grassia*, Theo.) so that the name *Pseudomyzomyia*, Theo., is incorrect, whilst a new name is required for what is now generally known as *Myzomyia*. In the present paper, however, the names in general use by Theobald are retained as being less confusing than new ones or old ones applied in a new sense.

Pm. rossi again is not comparable with the broad apical band in *N. maculatus.* (Plate V, fig. 14.)

Certain species, as previously mentioned, which normally or sometimes exhibit this condition (i.e., whitening of the whole apical segment) may at other times show a black band, due to incomplete extension of the apical pale area. The liability to this variation is not merely accidental. In the case of *Nyssorhynchus*, those species liable to the variation are distinctly related and exhibit affinities to *Cellia*. In *Myzomyia* incomplete extension of the apical white area is rare. It is more common in the heterodactylous *Pyretophorus*, e.g., *P. cinereus*, as a variation in *P. nursei*, etc.

A few species, all apparently related, show a peculiar variant of palpal banding, due to the absence of development of the apical pale area. These dark-tipped species which show three bands are *M. turkhudi*, Liston, *M. hispaniola*, Theo., *P. myzomifacies*, Theo., and *P. chaudoyei*, Theo.

In *M. turkhudi* this character is liable to some variation, the dark tip not being always very clearly shown.

Scheme C. So far, the only leucogenetic centre that has shown active spreading properties is that at the apex of the terminal segment. Another type of palp is seen in which the centres at both ends of the penultimate segment and at the apex of the second segment also become active. In this case whitening spreads up and down the shafts of the segments to produce the appearance seen in *N. maculatus* (Plate V, fig. 14). Here the residual pigment area is displayed as occupying almost the exact middle of the segment. The apical white band in such a case is not comparable with what looks like a very similar band in the case of *Pm. rossi*, etc.

Variation here usually consists in a partial, or more rarely in a complete effacement of the pigment centre on the penultimate segment.

Scheme D. What seems to be essentially a distinct scheme of ornamentation to any of the above, is one which may be described as showing in each segment only one apically situated leucogenetic centre and a basally situated residual pigment area. Species showing this type of palpal ornamentation are chiefly included under the many-spotted-winged species of Donitz, i.e., *M. punctulata*, *Nm. elegans*, *N. annulipes*, etc.

The scheme is beautifully demonstrated in *Ch. kochi*, Donitz, and it is apparently that on which the palpal ornamentation of *N. karwari*, James and Liston, is based (vide Plate V, fig. 15). The condition is very distinct from that ordinarily seen in *Nyssorhynchus*.

Possibly other variations or schemes of palpal ornamentation exist, but enough has been said to show the nature of the condition present in the great majority of species.

Markings of the legs. The occurrence of pale areas at the terminations of the femur, tibia and first tarsus is usual, and such may be conveniently termed '*knee spots*.' Except as an unusual variation, knee spots appear to be absent only in *Stethomyia*.

The occurrence of pale areas at the termination of the tarsal segments gives rise to an appearance which may be called *tarsal banding*. Tarsal banding may be of several kinds, depending upon whether the banding is a mere trace not very definite and confined to the actual joint, or whether it is broad and distinct involving an appreciable extent of the ends of the segments. In some cases, though banding is narrow, it is (as in *P. jeyporensis*) very distinct. In the case of broad banding, there are again two conditions depending upon whether the light area is merely somewhat paler than the rest of the segment or is pure white. The latter condition is, of course, much more conspicuous.

In some species the tips of the hind legs (and very rarely those of other legs) are white. This may be a condition in which there is a large continuous white area (as in *N. fuliginosus*, *My. paludis*, etc.), or one in which the whole tarsus shows alternate dark and light bands, one of which includes the tip. In the former case it will be found that two or three segments are completely devoid of any dark scales. In the latter case, though the terminal segment may be all white, the other segments still have some portion of their extent dark. In some cases, though the tip is white, not even one segment is altogether white, the terminal portion of white consisting in this case, as a rule, of a half or less, of the last tarsal segment. In separation of species the exact details regarding the number of segments white is important, but in the present paper, dealing somewhat broadly with the subject, I shall refer to two conditions only, i.e., (*a*) a continuous area of white involving at least two segments; (*b*) an interrupted black and white appearance of the tarsus in which the tip is white (i.e., as in *N. maculatus*, Theo.).

In the case of the tarsus of certain Culicinae there may be a development of pale areas at both ends of the segment or at one or other end only, so that there results apical and basal, apical, or basal banding as the case may be. Seeing how important the coloration scheme appears to be, such distinctions may have a good deal more systematic importance than one might be ready to grant at first sight. So far I have not sufficiently studied the nature of broad tarsal banding, and for the present shall not lay any stress on differences in this respect. In many species, however, the banding is purely apical, whilst in *Pm. rossi*, for example, it is distinctly apical and basal.

The condition called speckling is one in which distinct spots or bands are produced on the tibia or femur. Under an objective a certain amount of admixture of dark and light scales is often seen, and this may lead to a 'mottled' appearance under a lens. This is quite distinct from the defined spots and bands referred to as speckling. Speckling signifies a high degree of ornamentation and is usually associated with tarsal banding and, very frequently, with a white tipped tarsus.

An absence of speckling is characteristic of *Myzomyia* and of the *superpictus* group of *Pyretophorus*. Speckled species of *Pyretophorus* seem to be in many ways distinct from the latter group. Note, for example, *P. ardensis*, Theo., with 'furry' palps resembling those of a *Nyssorhynchus*, and the highly ornamented *P. aureosquamiger*, Theo. *Vide* also remarks on the scale structure and palpal characters of *P. costalis*.

In *Nyssorhynchus* speckling is the rule, and reaches a high degree of perfection. In *Anopheles*, *Myzorhynchus* and *Patagiamyia*, speckling is absent, but it is developed in *Cycloleppteron*, evidently a specialised but closely related genus to *Myzorhynchus*.

Ornamentation of the wing in Anopheles. The study of wing markings is complicated by the number of veins which may bear spots, the fact that the arrangement of spots on each vein may vary and that combinations are possible.

II. ORNAMENTATION OF THE WING IN *ANOPHELINAE*

As is well known, only the veins in mosquitos carry scales, and any spots that may be present are, therefore, restricted to these structures, and are linear in shape.

In this respect the spots on Anopheles differ from those in butterflies, not only in being linear, but in the fact that the spots in butterflies, as has been shown by Mayer,[2] originate on the wing between the veins, and only involve the veins by extension.

In the Nematocera two types of spots are seen (*a*) dark spots situated around vein junctions, and (*b*) dark wavy bands with serpiginous edges which extend across the wing. These often look as if their wavy margins had been caused by encroachment of pale areas developed between the veins.

The former type of spots are constantly encountered. On page 92, for example, of Theobald's Monograph, Vol. I, is figured a wing of *Rhyphus* in which dark patches are seen (1) at the junction of the subcosta with the costa, (2) at the junction of the first and upper branch of the second with the wing edge, (3) at the termination of the lower branch of the second, (4) at the cross vein linking the second with the next vein, and at two other junctions.

The most striking development of pale spots forming between the veins, and dark spots in connection with vein junctions I have seen has been in the case of certain species of spotted-winged *Chironomus*. In these species both wing membrane and vein is covered with minute hairs not unlike scales, and so the condition approaches that seen in Anophelines, whilst it seems to show what the primitive condition may have been. In these wings the two conditions seen are (1) aggregations of the hairs (or scales) in dense patches in the neighbourhood of the main cross veins and at two areas which seem to represent the bifurcation of the second and fourth longitudinal veins, and (2) distinct pale eye-like spots which occur on the wing membrane and have the minute scales covering them also pale (Plate VI, fig. 4). In one species examined there was a complete series of such spots occupying the cells and ranging along the whole outer and posterior aspect of the wing.

I have described these conditions at some length because

I believe they help one to understand certain of the facts to be described in the case of Anophelines, and because they seem to show so distinctly the primitive character of scale aggregation at the cross veins, and the actual existence of something very like my leucogenetic centres.

Primitive spotting in Anophelinae. The spotting seen on the wings of Anopheles is of two kinds:

(*a*) Spots due to special aggregations of scales;

(*b*) Spots due to alternate areas of light and dark scales.

The first type of spotting is very familiar in the case of the wings of *A. maculipennis*, Meigen. In this species no pale scales are present on the wing veins, but there are aggregations of scales forming dark spots. Such aggregations occur at the origin of the second longitudinal, at the origin of the third longitudinal, to a less extent on the neighbouring parts of the fourth and fifth veins (i.e., in the neighbourhood of the cross veins), and at the bifurcation of the second and fourth veins. This type of spotting is conspicuous in *A. maculipennis*, because the wings are devoid of other markings; but it is by no means confined to this species or to species with unspotted wings, and it occurs through a wide series of Anophelines, often along with considerable ornamentation of the second type of spotting. As it is seen chiefly (if not entirely) in what I shall show reason to believe are certain primitive groups, and as it is quite distinct from the spotting due to pale and dark scales, and as something very like it occurs in other groups than the Culicidae, I have called this *primitive spotting*. All species of *Myzorhynchus* which I have examined show it, also *Cycloleppteron grabhamii*, Theo. It is very plainly to be seen in *Pt. lindesayi*, Giles, and is prominent in *L. asiatica*, Leicester.

The species *P. atratipes*, Skuse, has an unspotted costa, its palps are unbanded, and it shows very marked and prominent primitive spotting. It clearly cannot be a *Pyretophorus*, and the certainty with which one can speak is a good example of the value of colour markings in systematic work upon the Anophelinae.

Scale clusters. In *Myzorhynchus* and *Cycloleppteron* there is a condition allied to this primitive spotting, in which dark spots on the veins are formed by scales larger than those on the light areas. Such areas of large scales are seen, especially on the sixth vein, forming the two dark spots characteristic of these genera.

Representation of spots on the lower surface of the wing. The veins of Anophelines carry scales on both surfaces. The character of the scales carried on each depends, however, on the particular vein concerned. In all Anophelines that I have examined, the upper surface of the first, third, fifth and sixth longitudinal veins carries blunt appressed, and what may be described as *flat scales*. On the under surface, all these veins (where they have scales at all) carry quite a different kind of scale, which in most Anophelines is pointed, and projects freely from the vein. The arrangement of scales carried by the second and fourth vein is reversed, flat scales being present on the under and projecting ones on the upper surface. What have been called lateral wing scales are, for the most part, simply the projecting scales on one or other aspect of the vein, as the case may be. As the end of the wing is approached, i.e., about the level of the forks of the second and fourth, the flat scales become increasingly long and projecting, so that in this position both surfaces of the wing carry projecting scales. This accounts for the appearance of the spots in this region which have a blurred look.

Except for a patch of scales towards its free end, or at most, over half its length, the sixth vein is devoid of scales on the lower surface of the wing. The main fifth and the inner part of the branch are similarly bare underneath. The result is that spots on these veins are very distinct and, under an objective, appear to be formed of special small flattened scales. The remaining veins carry scales on both surfaces.

On the whole, the upper surface of the wing is the more heavily scaled, and partly on this account, and partly owing to the preponderance of flat scales, the colour markings are, as a rule, more intensely represented on the upper than on the under surface.

In most Anophelines, allowing for the somewhat more intense coloration of the upper surface and the scale characters noted, the spots on the upper and under surface correspond. But in certain groups there is a marked lack of pale areas on the under surface corresponding with those on the upper, which may reach such an extent that the *under* surface of the wing is practically dark scaled throughout. A good test of this condition is the third longitudinal, which is most frequently a pale vein. In species where want of correspondence of coloration is marked, the pale, flat scales on the upper surface of this vein will be seen to be flanked by dark lateral scales (i.e., ventral scales), seen through the membrane.

This appearance, called admixture of dark and light scales, has often been referred to, but, so far as I know, no one has previously realised its nature or significance. The group in which dark scaling of the under surface of the wing reaches its most striking development is the *Myzorhynchus* group, including *Cycloleppteron* and *Arribalzagia*.

A rather interesting condition was noted in the halteres of a specimen of *Cycloleppteron mediopunctatus*, which showed, distinctly, the appearance of an unexpanded wing. These structures were covered with snowy white scales on the upper surface, with a central dark spot, but on the under surface were clothed with deep black scales.

The wing of *Myzorhynchella nigra*, Theo., is almost entirely dark scaled beneath, though it has many pale spots on the upper surface; also many pale spots present on the upper surface are lacking on the lower in *P. watsonii*, Leicester (*Myzorhynchus*?) a species allied to *My.* (?) *natalensis*, Hill and Haydon, as well as in *Nm. elegans*, James. *Cellia squamosa*, Theo., and *M. lutzi*, Theo., show a third longitudinal, light above and dark below. *P. atratipes*, Skuse, is another species in which the wing is almost entirely dark scaled beneath, though it carries quite conspicuous pale areas on the second, fourth, fifth and sixth veins above.

In *Pt. gigas* and *Pt. simlensis* the markings are, for the most part, reproduced on the lower surface of the wing.

In *Myzomyia*, *Pyretophorus*, *Nyssorhynchus* and in *Cellia pulcherrima*, Theo, the wing spotting is equally represented on both surfaces, though in some 'dark' *Nyssorhynchus* dusky scales, not definitely dark or light, may be present beneath the third vein.

Admixture of dark and light scales. Apart from the effect of admixture, due to the showing through of dark scales beneath the wing membrane, there is in *Myzorhynchus*, *Cycloleppteron* and *Arribalzagia* a true occurrence of mixed black and pale scales on many of the veins. Such admixture of scales is not seen in the majority of Anophelines, and does not occur, so far as I am aware, in *Myzomyia*, *Pyretophorus*, *Nyssorhynchus* or *Cellia*.

All the characters so far mentioned must be looked upon as special to certain groups of Anophelines. What one may call the more ordinary Anophelines show neither primitive spotting, nor any degree of unequal ornamentation of the wing surfaces, nor admixture of light and dark scales on the veins, and in them spotting depends entirely upon the existence of definite areas of pale and dark scales on the veins.

Another condition of possible importance, but concerning which my observations are too imperfect to enable me to deal, is staining of the wing membrane in the area of dark spots. This is greatly exaggerated in *Cycloleppteron mediopunctatus*, but is seen in many species.

Nodal Leucogenetic Centres of the Wing

The wings exhibit very clearly a system of leucogenetic centres and residual pigment areas. The leucogenetic centres are of two kinds, those associated with what may be called '*nodal points*' of the wing, and those which I shall call '*internodal*.'

The nodal points in the wing of an Anopheline which have relation to spotting are shown by the small circles in Plate VI, fig. 1. They may be enumerated as follows:—

(1) The apical nodal point at the junction of the first longitudinal vein with the costa (*Ap.*).

(2) The subcostal nodal point at the junction of the subcostal vein with the costa (*S.c.*).

(3) The humeral nodal point where the humeral cross vein enters the costa near its base (*h.*).

(4) Nodal points in connection with the cross veins (C_2-C_5).

(5) Nodal points at the bases of the forked cells (bifurcation of veins two and four).

(6) Nodal points at the junction of all veins and their branches with the wing margin.

There are other points whose nodal origin is possible or probable. These are:—

(7) A point on the first longitudinal vein slightly internal to

the termination of the second longitudinal. If, instead of being joined to the first longitudinal by a cross vein (cross vein 2), the second longitudinal itself formed a direct junction with this vein (*Vide* remarks on wing venation in Section III), it would presumably enter at the nodal point in question. Some authors figure the vein as acting in this way; but I have not found any example of an Anopheline wing showing this arrangement. On the other hand, it appears to occur in some other Culicidae (occasionally in the case of *Theobaldia annulata*). The nodal point in question is an important one, and, as it occurs at the origin of the Sector radius vein, I have called it the *Sector nodal point* (*S*). The nodal point at the entrance of the cross vein actually linking on the Radio-Sector, which is also a very important one in relation to wing markings, may be called the *Accessory Sector* (*S'*).

(8) It is possible that a nodal point occurs on the first longitudinal at *C*.1.″ in the diagram. In Anophelines, no sign of any cross vein exists here, but such a cross vein is commonly seen in Tipulids (*Vide* Plate VI, fig. 2). Another possible nodal point is at *C*.1′. Breaking of the subapical costal spot in *P. costalis*, and some other species, also suggests a point of a nodal character, marked with a (?) in the diagram.

These points behave as nodal points, and it is possible that a study of the developing wing in the nymph may throw light on their origin. But at present their structural origin can only be suspected.

It is noticeable in regard to white areas formed at the nodal points, that they do not show so active a tendency to spread as do those of an internodal character.

Species showing 'dark' or 'light' areas at the cross veins and bifurcations. Certain nodal points may be represented by a leucogenetic centre or by a pigment centre. The nodal points on the costa rarely exhibit the latter condition, but the humeral junction is not infrequently the site of a pigment spot (instead of a pale spot), as in *Cycloleppteron grabhamii*. Still more rarely, the junction of the subcostal vein may be the site of a dark spot, *Cy. mediopunctatus* and *Ar. maculipes*, whilst a dark spot in close association with this junction is seen in *Nm. elegans*, *M. punctulata* and *N. annulipes*, Walker. Such spots form small accessory spots on the costa (apart from the basal accessory spots to be described later), and are possibly of much greater significance than their mere size might suggest.

The nodal points of greatest importance in connection with their power to be either ' dark ' or ' light ' are those at the cross veins and bases of the cells. In the genera *Myzomyia*, *Pyretophorus*, *Nyssorhynchus*, *Cellia*, and *Neomyzomyia*, the cross veins are always the site of light interruptions. In *Myzorhynchus*, *Patagiamyia*, *Cyclolcppteron*, *Arribalzagia*, and *Myzorhnychella* these areas not only are dark, but, when given the chance, exhibit themselves as residual pigment centres. In a great many cases, in addition, they are the site of scale aggregations, giving rise to primitive spots (*Vide* Plate VIII, figs. 1-13).

Nodal points on the costa and first longitudinal. In those species with unspotted costa, we may consider that none of the nodal leucogenetic centres have displayed themselves. This is the typical condition in *Anopheles*, restricting this term to the genus as defined by James (i.e., without a prothoracic tuft). It is also the condition in *Stethomyia*.

The first nodal leucogenetic centre to become evident in all other species, without exception, is the *apical*, giving rise to the condition seen in *Pt. lindesayi* and *P. atratipes*.

The next nodal centre to appear is invariably the *subcostal*. This is the typical condition in *Myzorhynchus*, though in some species (*My. sinensis*, *My. pseudopictus*) the sector spot has also made its appearance on the first longitudinal, but has not spread on to the costa. The same condition is seen in *L. asiatica* and in the related form *My. wellingtonianus*, Alcock.

The third nodal centre to appear as a pale spot is either the *sector spot* or the *humeral spot*, usually together with a spot at the extreme base of the wing and at the (? nodal) point *C*.1.'

If the sector spot becomes prominent without the others there results the *sinensis* type of wing. If the sector spot remains in abeyance and others develop, the *gigas* and *punctipennis* type of wing is produced (Plate VIII, figs. 9 and 4).

So far, all species showing no further elaboration of the costal spotting than that described, have dark cross vein areas, frequently exhibit primitive spotting and a scheme of wing ornamentation in regard to internodal spots, which is distinct from that seen in *Myzomyia*, *Pyretophorus*, etc.

The sector spot and the (?) nodal spot at *C*.I.″ appear in most cases simultaneously, giving rise to a four spotted costa. The condition in *Cycloleppteron grabhamii* is that shown in *Myzorhynchus*. In the case of *C. mediopunctatus*, the sector spot has included the costa, pale areas have appeared at the base, and the extent of the dark scaled portion is less. In *Arribalzagia maculipes* the dark costal spots are still more sharply differentiated and restricted. Both these greatly modified wings appear to be distinctly a development of the *Myzorhynchus* pattern. In *Myzomyia*, *Pyretophorus*, *Nyssorhynchus*, *Neocellia*, and *Cellia*, the costal pattern, except as the result of occasional individual or specific (?) variation, shows four main spots due to the formation of pale centres at the apical, subapical, subcostal, and sector nodal points, respectively. In the great majority there is also a pale area at the humeral, at the base of the wing, and at *C*.I.′. The accessory sector spot may be blended with the sector spot, merely shortening a little the middle spot as represented on the first longitudinal vein (e.g., *M. culifacies*). It may be lost in the general extension of the sector spot (e.g., certain *Pyretophorus*), or it may form a distinct interruption towards the inner side of the middle dark costal spot, as is the case throughout *Nyssorhynchus*. In most *Nyssorhynchus* a very similar interruption is also seen towards the outer end of the spot. The exact origin of this second interruption is uncertain, but it lies opposite the junction of the third cross vein with the stem of the second longitudinal. Where the inner interruption only is present, I shall speak of the middle costal spot as being 'incompletely broken,' where both interruptions are seen, I shall refer to this spot as 'completely broken' (Plate VIII, figs. 34, 37).

In certain species one or both of the small dark scaled portions on the first longitudinal, separated off by the pale interruptions, may have disappeared. The disappearance of both small spots gives what is frequently spoken of as the 'T' shaped spot of *Pm. rossi*.

The same kind of interruption may occur, but not commonly, on the first longitudinal, under the subapical dark costal spot.

This is very characteristic of *P. costalis*, and is seen particularly in the many-spotted winged species. It can be referred to as a broken subapical spot. (Plate VIII, fig. 25.)

Accessory costal spots. On the costa at the base of the wing are very commonly seen from one to three small dark spots which as a rule are unrepresented on the first longitudinal or even on the subcosta. These may conveniently be termed *basal accessory spots.* In *Myzomyia*, *Pyretophorus*, *Nyssorhynchus*, etc., two such spots are most commonly seen lying on either side of the junction of the humeral cross vein; but three are sometimes present, and not infrequently they may join together among themselves, or, either in part or wholly, be linked on to the inner main costal spot, giving the appearance commonly seen in *M. listoni.* (Plate VIII, fig. 28.)

Another type of basal accessory spot is sometimes seen where the dark area occurs at the junction of the humeral cross vein, e.g., *Cycloleppteron mediopunctatus.*

The number and arrangement of accessory basal spots, or whether any light areas exist at all on this part of the costa, does not seem to be very important.

The selection of the site of junction of the humeral vein for a dark spot is, however, very significant.

Accessory costal spots other than the basal accessory spots are found in certain cases. These appear to be of considerable significance, and their exact site is very important. The mode of formation and homology of such spots in different species can be traced. In *Ch. kochi*, Donitz., a prominent accessory spot is seen on the costa between the inner and middle dark costal spot. The nature of this spot is clearly shown by a study of the wings of *P. watsonii*, Leicester, and of *My. natalensis*, Hill and Haydon. The wing of *My* (?) *natalensis*, as shown in the photograph given by its describers, is a beautiful demonstration of the typical subdivision of the costa into dark spots by the appearance of the apical, subcostal, sector, accessory sector and *C*.I.″ nodal leucogenetic centres. In the species *P. watsonii*, Leicester, the type of which is in the British Museum, a very similar arrangement of spotting is shown, but the accessory sector spot has developed to such an extent as to reach the costa, forming a small detached dark spot clearly identical with that seen in *Ch. kochi.* This fact is the more interesting in that such a spot is not common in Anophelinae, and that it is for the most part seen in the many-spotted-winged species, e.g., *Nm. leucosphyrus*, Donitz. *P. watsonii* and *My. natalensis* show therefore very curious affinities; showing an approach to *Myzorhynchus* they so far differ as to have been excluded, or to have been regarded as doubtfully belonging to this genus, by their describers; they distinctly recall some *Patagiamyia* characters and as pointed out they have some unusual points in common with the many-spotted-winged group and with *Ch. kochi*, Donitz, which species it should be remembered has *Myzorhynchus*-like wing scales.

Bridging of costal spots on the first longitudinal. Certain species, including *C. squamosa*, Theo., *C. albimana*, Wied., and *N. fuliginosus*, Giles, show a bridging of certain of the pale costal areas by dark areas on the first longitudinal. The same feature is displayed in *Myzorhynchella nigra*, Theo. The species *Myzorhynchella nigra* shows a four-spotted costa; it has a wing with a fair number of markings above, but almost entirely dark-scaled below; the cross vein nodal points are dark; it has prothoracic tufts; there can be little doubt but that it is related to *Myzorhynchus*. If, as seems possible, *C. squamosa*, which exhibits distinct *Myzorhynchus*-like affinities, really descended from a primitive *Myzorhynchus*-like ancestor, one would expect this form to be something like *Myzorhynchella*, though the evidence for such a descent, and for that tentatively suggested for the *elegans* group, is very slender.

Nodal points on wing margin. When pale spots display themselves in this situation they affect not only the veins but also the wing fringe, forming 'pale fringe spots.' The amount of possible spread of these spots, like most other spots of nodal origin, is small.

Internodal Leucogenetic Centres of the Wing

The internodal spots appear as a rule almost exactly in the centre of long stretches of dark vein lying between nodal points, and the order of appearance of the internodal spots has a distinct relation to the length of the dark area concerned. The internodal points in the scheme of coloration shown by *Myzomyia*, *Pyretophorus*, *Nyssorhynchus*, etc., are:—

(1) One on the upper branch of the second (2^1). Two on the lower branch (2^2 and 2^3). These are usually so placed that they alternate, as shown in the diagram, and the result is that the limbs of this forked cell are *asymetrically* marked.

(2) On the shaft of the third vein. Whether one or two centres are here concerned is not quite certain, but I am inclined to think that there are two which very readily blend (*vide* appearance shown in some species).

(3) One on the upper branch of the fourth vein (4^1). One on the lower branch (4^2). In this case the branches are marked symmetrically, though owing to the slope of the wing edge the actual position of the spots is not quite opposite one another.

(4) One on the upper branch of the fifth, i.e., between the nodes *C*.5. and $5'$. Two on the main branch of the fifth, one above and one below the junction of the branch.

(5) Two on the sixth, dividing this vein approximately into three portions.

Not only have these internodal centres a nearly fixed position, but they have an almost fixed order in which they become apparent by the development of pale spots.

The internodal spots, once they appear, tend to extend very rapidly along the veins, causing much more extended pale areas than do the nodal points.

The first spot to appear is 5^1 on the main fifth beyond the fork. In certain species this is the only internodal spot present (e.g., *funesta* var. *umbrosa*). In *M. culicifacies*, *M. nili*, etc., this is also the only conspicuous spot present.

The next spot to appear is generally one of those on the third vein, giving rise to a variety of *M. culicifacies* and *M. funesta* var. *subumbrosa*, with more or less pale third longitudinal. In association with this appears a spot on the upper portion of the fifth (5^2), and a pale area at the base of the fourth longitudinal (4). The wing at this stage of ornamentation is that seen in the lighter-winged *Myzomyias*, i.e., *M. listoni*, *M. funesta*, etc. The only *Myzomyia* (excluding certain forms previously mentioned) which shows any further ornamentation is *M. albirostris*, Theo. (*M. aconita*, Donitz ?), a peculiar species in many respects, including the larval characters.

With a further degree of lightening of the wing, additional spots appear at 5^2 on the branch of the fifth, and on the forked cells, 2^3 being a little later in appearance than the others. Whilst these areas have, as it were, only just appeared, the ones previously noted have spread considerably, so that as a rule the third vein is completely pale, for example, in any species showing a pale spot at 5^2.

The scheme so far developed is that seen in a number of species of *Pyretophorus;* though in other species of this genus an additional spot (6^2) has appeared.

The nodal points on the edge of the wing behave in concert with this progression. In the wings showing only 5^1 the fringe spots are generally deficient (e.g., two in *M. culicifacies*). In association with the appearance of the nodal centres 3 and 5^2, fringe spots are generally found at all veins except the sixth. The nodal point at the termination of this last vein only occurs as a rule after 6^2 has appeared. At about the same time another (?) nodal spot not previously represented forms a pale area on the first longitudinal, opposite cross vein 3. It is this which gives the double break in the middle costal spot so characteristic of *Nyssorhynchus*, etc.

Whilst no further internodal spots appear, the wing still continues to show modifications owing to the encroachment upon, and in some cases obliteration of, residual pigment areas. The more important changes produced by this extension of the internodal centres are (*a*) the blending of 5^1 and 5^2, thus producing the commonest condition of the fifth vein in Anophelines (*vide* Plate VII, fig. 4); (*b*) the obliteration of one or both of the small spots on the first longitudinal under the main spot (points of the 'T' in *rossi*); (*c*) obliteration of one of the dark spots on the sixth vein, either the upper or the middle one as in some species of *Cellia*; (*d*) obliteration of one or more of the small dark spots on the forked cells (usually the first to go is $2'' b$, the next most usually $2' b$ or $4'' b$); (*e*) the obliteration of the dark spot $4r$.

In addition to mere extent of white involved there is a difference in the intensity of the colour. Roughly speaking, *Myzomyia* and *Pyretophorus* show *pale* but not markedly *white* areas. *Nyssorhynchus* and *Cellia* exhibit a striking dead-white ornamentation.

In *Myzorhynchus*, *Cycloleppteron*, *Patagiamyia*, etc., some of the internodal centres appear to be the same as certain of those described, but there is no general correspondence in the scheme of coloration. Also in this group there seems to be a much less orderly sequence of such pale areas as do appear. The whole effect of the ornamentation is of course modified by the fact that the cross vein nodal centres are dark.

A group showing light nodal centres, but having a wing ornamentation scheme absolutely without relation to that of *Myzomyia*, etc., is the group Donitz[4] has drawn attention to as markedly peculiar owing to the character of the wing spotting. The most striking character of the wing in this case is the extraordinary multiplication of spots due to alternate short lengths of dark and light scaling on the veins. Practically none of the internodal areas seen so regularly throughout *Myzomyia*, *Pyretophorus*, etc., can here be made out. The sixth vein shows from four to six dark areas, the main fifth at least three interruptions on each portion of the stem and on the branch respectively. The branches of the second and fourth veins have each a double interruption. The third, instead of being throughout most of its length either dark or pale, is broken up into alternate light and dark areas.

Summarising what has been detailed above, we can say that there are three absolutely distinct colour schemes on which the spotting of wings of Anophelines is modelled. These are:—

(1) Scheme A. The scheme on which the wings of most ordinary Anophelines are spotted, characterised by the very regular appearance in a definite sequence of certain internodal pale spots and by the cross veins and bifurcation nodal points being pale.

(2) Scheme B. A less regular scheme shown by *Myzorhynchus*, *Cycloleppteron*, *Patagiamyia*, etc., in which the nodal points at the cross veins and bifurcations are dark.

(3) Scheme C. A scheme characterised by multiple spotting of the veins and the occurrence of more than three dark spots on the sixth.

These three schemes not only seem of the most fundamental importance, but as displayed in the great majority of species of Anopheles can be distinguished at a glance.

Variation in Colour Marking shown by Individuals of the same Species

In any attempt to utilise colour markings as a basis of classification the question of individual variation must be considered. It may be objected that such variation as is displayed in many species will prevent use being made of colour markings. This I think is not necessarily so, because variations shown by individuals of the same species have only a certain latitude, and with a correct appreciation of what a given variation really amounts to one is able to allow for variation in classification. The appearance of a new centre out of its order, or the change of the markings over several steps of normal colour marking development, would be a much more serious matter than the final extinction of a disappearing pigment area or the appearance of a pale centre already on the point of appearing. In this respect I believe a knowledge of the principles underlying colour marking will give an added importance to observations upon individual variations. Certain stages seem distinctly unstable, others much more stable. The knowledge as to the relative stability of different conditions cannot but be of value in deciding whether certain forms are species or varieties.

III. VARIATION IN STRUCTURE OTHER THAN THAT CONNECTED WITH SCALES

Very few structural variations other than those connected with scales are mentioned in descriptions of species of Anophelinae. This is in itself rather suggestive that such variations as do occur are not of an obtrusive nature. So far as I can ascertain the following are almost the only points in which different species of Anophelines differ from one another in respect to structure.

General shape of body. Donitz[4] has called attention to certain characters of the head and the shape of the thorax in Anophelinae. These require fresh material for proper study, and my observations in this respect do not add anything to what was previously known.

Closely associated with the general shape of the body is the attitude adopted by the species when at rest. The most importance attaches to the possession of a '*culex*'-like attitude. This attitude seems to be a definite character of *Stethomyias*. *M. culicifacies*, Giles, and *Chagasia fajardoi*, Cruz, are the only species apart from this group which, so far as I know, have been described as adopting this attitude. The '*culex*' attitude in the former is not nearly so striking as in the case of *S. aitkeni*, which superficially almost exactly resembles some long-legged *Aedine* mosquito.

Apart from the assumption or not of the '*culex*' attitude, there are marked differences in the angle made by different species with the surface on which they are at rest. Observations in this respect are too limited to allow any general conclusions being drawn as to any possible significance attitude may possess in respect to generic affinities.

The antennae. In the female antenna the arrangement of the segments in respect to their length is somewhat peculiar. Following upon the large globular basal (second segment according to Nuttall) is a rather long segment. The next segment is in most species not only the shortest in the whole antenna, but is often almost or quite globular. In *My. barbirostris*, *My. umbrosus*, *My. paludis*, *My. sinensis* and *C. grabhamii*, though this segment is still the shortest in the antenna it is not nearly so disproportionately shortened, nor has it the same globular appearance as in most Anophelines. The segment is also rather longer than usual in *P. jeyporensis*, James.

The male antenna possesses a very striking structural peculiarity in the great length of the two terminal segments. But so far as I could see the relative lengths of these structures exhibited very little change in different species, nor do the antennae of different species differ noticeably in other respects.

Female palpi. The number of articulated segments in the female palps in Anophelines is four. There is, however, a vestigial prominence carrying tufts of scales at the extreme base of the palps which probably represent a fifth segment.

Distinct variations occur in the relative length of the different segments. In this respect two types of palps can be distinguished, which I have termed respectively *orthodactylous* and *heterodactylous*.

In the first or *orthodactylous* palps the segments observe a kind of proportionate decrease in size as the apex of the organ is approached. In the very orthodactylous genera, such as *Myzorhynchus*, the terminal segment may be as much as two-thirds the length of the penultimate. One may define an orthodactylous palp as one in which, whilst the segments one and two keep their proportionate length (they only vary to any extent in *Stethomyia*), the last segment is not less than half the length of the penultimate segment.

In the second or *heterodactylous* type of palp there is a marked want of regularity in the decrease exhibited by the segments. Of heterodactylous palps two distinct types are encountered, due to the disproportionate length of the preapical and second palpal segment respectively.

Great increase in the length of the preapical segment is seen in both *Myzomyia* and *Pyretophorus*, the apical segment being a third or even a quarter of the preapical (Plate V, fig. 10). Such a marked structural variation in a sub-family otherwise showing very few changes in structure must have considerable significance. Species with distinctly orthodactylous palps now included in these genera, e.g., *P. costalis*, Loew., would seem to require separation.

The second type of heterodactylous palps occurs in *Stethomyia*. In this case the second segment is very long and the third disproportionately short (Plate V, fig. 16). This variation is the more remarkable in that amongst other Anophelines any marked change in the relative length of the first and second segments is conspicuously absent. This type of palp cannot be overlooked, if attention is directed to it, and it would seem in itself a sufficient and very good generic character. As previously mentioned, *S. corethroides* shows the linear head scales characteristic of *S. aitkeni*. It also shows the peculiar modification of the palps mentioned above. A similar condition of the palp is figured by Theobald for *S. nimba*.

Expressing the relationship of the terminal to the penultimate segment in a decimal, one can obtain, when dealing with orthodactylous palps or with the first type of heterodactylous palp, a very useful index. What may be called the palpal index for a number of species is given below. This index can be determined very accurately from balsam-mounted specimens by direct measurement with an eye-piece micrometer, but better by making camera lucida drawings, taking care to avoid any possibility of distortion. Those indices given in the table where no other remark is made have been determined in this way and checked by direct measurement.

Species	Palpal index	Source of information
My. barbirostris	0·61	Mounted specimen
My. umbrosus	0·69	,,
My. mauritianus	0·55	,,
Cy. grabhamii	0·70	,,
A. maculipennis	0·57	,,
A. bifurcatus	0·50	,,
Pt. lindesayi	0·71	,,
M. funesta	0·32	,,
P. nursei	0·32	,,
P. cleopatrae	0·35	,,
P. jeyporensis	0·32	,,
Pm. rossi	0·50	,,
P. costalis	0·75	,,
N. fuliginosus	0·60	,,
Ne. fowleri	0·62	,,
N. maculatus	0·50	,,
C. pulcherrima	0·54	,,
C. squamosa	0·68	,,
C. albimana	0·79	Specimen not mounted
M. aconita	0·43	From Donitz's figures
M. hebes	0·33	,,
M. deceptor	0·59	,,
Nm. leucosphyrus	0·68	,,
M. punctulata	0·63	,,
M. tenebrosa	0·73	,,
N. maculatus	0·50	,,
N. leucopus	0·46—0·57	,,
P. cinereus	0·37	Photo by Hill & Haydon
P. ardensis	0·75	,,
My. natalensis	0·76	,,

Given a good photograph, one can usually make a rough determination of the palpal index; very often, however, a glance will tell one whether a particular palp is orthodactylous or distinctly heterodactylous.

In the drawings given in the Plate the palps of different species have been drawn by means of a Zeiss adjustable lens (a^*), so that they are shown of the same size (not scale). This shows very clearly the variations in the proportions of the different segments. The extremely low index of *Myzomyia* and the *nursei* group of *Pyretophorus* is practically diagnostic.

The male palpi. These show a change more or less analogous to that seen in the female, the palp being more abruptly clubbed and the last two segments taken together measuring proportionately less in the heterodactylous species than in others.

The wings. On the whole the structural characters of the wings are more interesting from their fixed character than for the variations they exhibit. Two conditions have, however, been made use of as variables by Theobald and others. These are the positions of the cross veins and the length of the forked cells. On these subjects I have nothing new to add.

Much more important from our present point of view are certain points connected with the homology of the wing venation in Anophelines. According to Comstock and Needham the generalised insect pattern of wing venation shows the following main longitudinal vein systems, the branches of which are represented more or less closely by tracheal branches which precede them in development: —

(1) The costa.
(2) The subcosta.
(3) The radial system.
(4) The medial system.
(5) The cubital system.
(6) Three anal veins.

The subcosta is normally a bifurcate vein, the branches of which enter the costa at two points. In many forms the lower branch becomes fused with the radius for a portion of its length, so that there appears to be (1) a branch joining the terminal portion of the subcosta with the radius, and (2) a branch going from the radius to the costa. The auxiliary or subcostal vein in Anophelines is an unbranched vein entering the costa a little beyond its middle. It seems quite clear that it is homologous with the subcosta of the generalised pattern, and it shows the *humeral cross vein* joining it and the costa near its base, which is a feature of the generalised wing.

The radius in its typical development consists of an unbroken vein R_1, passing from the base of the wing to the neighbourhood of the apex (Plate VI, fig. 2). Posteriorly to this there arises a branch (the *radio-sector*) which sub-divides into two branches R_{2+3} and R_{3+4}, each of which again sub-divides, forming four terminal branches R_2, R_3, R_4 and R_5. Between the lower branches of the radio-sector (R_{4+5}), and the medial system is the second of Comstock and Needham's cross veins, the *radio-medial*. Nuttall and Shipley consider the first longitudinal vein to be R_1, the branches of the second longitudinal to be R_2 and R_3 respectively, whilst the third longitudinal is the combined R_{4+5}. Following this homology the radio-sector will be that portion of the second longitudinal between its origin and the origin of the third vein, i.e., where the supernumerary cross vein enters it.

Some figures show the second longitudinal as a branch of the first. In reality, though it is joined near its origin to the first longitudinal by a cross vein, the vein itself continues past this a short distance to end on the wing membrane, as noted by Nuttall and Shipley. Presuming the second longitudinal to be homologous with the radio-sector, its true line of departure would be a little internal to the cross vein, a point we have referred to when discussing the formation of wing spots.

The division of the radio-sector into R_{2+3} and R_{4+5} would, following Nuttall and Shipley's homology, occur at the so-called supernumerary cross vein. Some authors figure the third vein as arising directly from the second, but this is not actually the case, and the junction is brought about by means of a cross vein, the vein itself continuing slightly beyond this to lose itself on the wing membrane.

The cross vein joining the third with the stem of the fourth vein would appear to be one of Comstock and Needham's original cross veins (radio-medial). The fourth longitudinal would appear to represent the median, the fifth longitudinal the cubitus, and the sixth the first anal.

The only cross veins in Anophelines actually represented as cross veins in Comstock and Needham's generalised nomenclature are (1) the humeral, (2) the medio-radial, (3) the radio-cubital, these being respectively the humeral, the mid and posterior cross veins of Theobald. But there are, as we have seen, additional cross veins which are quite indistinguishable structurally from the first-mentioned, and one of these (that linking the third with the second vein) is called the supernumerary by Theobald. The cross vein at the origin of the second vein, though noted by Nuttall and Shipley, has not received a name. Since it links up the radio-sector to R_1 it might appropriately be called the radio-sector cross vein. I would suggest, however, the use of the terms first, second, third, fourth and fifth as applied to the cross veins which makes no attempt, as is very imperfectly done at present, to denote their homology. It seems absurd to term the longitudinals by numbers and the much less important cross veins by a hybrid nomenclature only partially descriptive. The omission of the radio-sector cross vein, which is every bit as important as the others, is also absurd. In the following pages I shall refer to the cross veins according to the following plan, which has the merit that each vein has the same number as the longitudinal vein immediately behind it.

Homologous nomenclature	Present nomenclature	Suggested name	Position
Humeral	Humeral	Humeral or first	Joins costa to subcosta at base
(Radio-sector)	——	Second	Links on second vein
(Lower radial)	Supernumerary	Third	Links on third vein
Radio-medial	Mid-	Fourth	Joins fourth vein to third
Medio-cubital	Posterior	Fifth	Joins fifth to fourth

On the system suggested the cross veins entering any given vein can be at once named, or the veins that any cross vein affects be at once called to mind without effort.

IV. STRUCTURAL VARIATION IN THE IMMATURE STAGES

A considerable number of larval forms have now been described, and it seems possible to make some tentative use of the facts gathered in attempting to ascertain the affinities of species. In particular the variations in the antenna, i.e., whether it carries a branched hair or not, and the occurrence in certain species of the lanceolate type of palmate leaflet would seem to be significant. Variations in the frontal hairs and other features have been described for a number of species, but the application of such variations to classification is less obvious.

Species with a branched antennal hair. So far as I have been able to ascertain, the following species possess a well marked or vestigial branched antennal hair.

A. maculipennis, Meig. Noted by Hill and Haydon.

A. bifurcatus, Linn. *Vide* Plate.

Pt. lindesayi, Giles. Stephens and Christophers.

A. crucians, Wied. Smith.

Pt. punctipennis, Say. Smith.

Pt. simlensis, James. James.

My. sinensis, Wied. Stephens and Christophers.

My. barbirostris, Van der Wulp. Stephens and Christophers.

My. paludis, Theo. Hill and Haydon.

Chagasia fajardoi, Lutz. Shown in drawing of larva by Silva.

The larval antenna of *Cy. grabhamii*, Theo., is figured by Theobald without a branched hair. This structure can, however, be very readily overlooked if attention is not especially directed to it, and the observation requires confirmation. It is interesting to note that no branched hair is present in *My. natalensis*, Hill and Haydon.

Species with lanceolate type of palmate hair leaflet. The type of leaflet seen in *Myzorhynchus* is not uncommon. The following species have been described as showing lanceolate and serrated palmate leaflets.

A. maculipennis, Meig. Hill and Haydon.

A. bifurcatus, Linn. *Vide* Plate.

My. barbirostris, Van der Wulp. Stephens and Christophers.

My. sinensis, Weid. Stephens and Christophers.

My. paludis, Theo. Hill and Haydon.

Cy. grabhamii, Theo. Theobald.

C. albimana, Wied. Graham.

C. squamosa var. *arnoldi*, Steph. and Christop. Newstead and Carter.

C. albipes, Theo. Low.

Forms showing an approach to this type of leaflet, but in which the leaflet is drawn without serrations and as of a simple fusiform shape.

C. squamosa, Theo. By Hill and Haydon.

Myzorhynchella nigra, Theo. Silva.

Myzorhynchella parva, Chagas. Silva.

Stethomyia culiciformis, James. James.

Forms showing an approach to this type of leaflet in the serrations at the shoulder of the leaflet are more drawn out than in ordinary Anophelines has been noted in:—

My. (?) *natalensis*, Hill and Haydon. By these authors.

Pt. lindesayi, Giles. Stephens and Christophers.

S. aitkeni, James. By this author.

Nm. elegans, James. By this author.

P. ardensis, Theo. Hill and Haydon.

Hill and Haydon figure *N. pretoriensis* with leaflets of this character, but in the photograph accompanying their paper the condition is not so clearly shown.

The extreme degree of branching of the external frontal hairs characteristic of *My. sinensis* is also shown by *My. paludis* (Hill and Haydon). This character may therefore be reasonably taken as one of the features of *Myzorhynchus*. Its absence in any given species would draw attention to doubtful generic position. Marked feather-like branching resembling that in *N. fuliginosus*, Giles, is also seen in *C. squamosa* and in *C. pulcherrima*. The following tabular statement gives, as far as the information available allows, the chief larval characters of a number of species *arranged in the order of their apparent phylogenetic significance.*

Variations in the nymphal structure of Anophelines. Very little variation can be detected in the nymph of different species. There is, however, a slight but appreciable difference between the nymphal trumpets of *My. sinensis*, *My. barbirostris*, *Pt. simlensis*, *A. maculipennis* and *A. bifurcatus* and those of Anophelines

TABLE showing larval characters in order of apparent phylogenetic significance

	Branched hair on antenna + = present, O = absent.	Palmate leaflets lanceolate + + ; showing tendency as in lindesayi +	Palmate leaflets fusiform.	Palmate leaflets with ordinary longish filament.	Palmate leaflets with stumpy filament.	External frontal hair branched as in *Sinensis* B, as in *fuliginosus* bb, otherwise distinctly branched b, simple or with fine lateral branches S.
Stethomyia aitkeni	O	+				S
,, *culiciformis*	O		+			S
Anopheles maculipennis	+	+ +				B
,, *bifurcatus*	+	+ +				S
,, *eiseni*	+	?				S
,, *crucians*	+	?				S
Patagiamyia lindesayi	+	+				S
,, *simlensis*	+	?				S
,, *punctipennis*	+	?				S
Myzorhynchus sinensis	+	+ +				B
,, *barbirostris*	+	+ +				B
,, *paludis*	+	+ +				B
Cycloleppteron grabhamii	?	+ +				S
Chagasia fajardoi	+			+		
Myzorhynchus (?) *natalensis*	O	+				b
Neomyzomyia elegans	O	+				S
Cellia squamosa var. arnoldi	O	+ +				bb
,, *squamosa*	O		+			bb
,, *albimana*	O	+ +				
,, *albipes*	O	+ +				b
,, *pulcherrima*	O			+		bb
Pyretophorus ardensis	O	+				
Myzorhynchella nigra			+			
,, *parva*			+			
Nyssorhynchus fuliginosus	O			+		bb
,, *nivipes*	O			+		bb
,, *jamesi*	O			+		b
,, *maculipalpis*	O			+		b
,, *pretoriensis*	O					S
,, *maculatus*	O				+	S
,, *theobaldi*	O				+	S
,, *karwari*	O					
,, *willmori*	O				+	S
Christophersia kochi	O				+	S
Myzomyia culicifacies	O			+		S
,, *listoni*	O			+		S
,, *funesta*	O			+		S
,, *turkhudi*	O				+	S
,, *albirostris*	O					b
Pyretophorus cinereus	O			+		S
,, *nursei*	O			+		S
Pseudomyzomyia rossi	O			+		S
,, *ludlowi*	O			+		S
Pyretophorus jeyporensis	O			+		b
,, *costalis*	O			+		S
Cellia jacobi	O			+		S

belonging to the genera *Myzomyia*, *Nyssorhynchus*, etc., those of the former being more triangular in shape and less scoup-like than those of the latter. (*Vide* Plate V, figs. 1 and 2.)

V. VARIATION AS DISPLAYED BY SCALES

A detailed account of scale structure would be foreign to the purpose of this paper. But it is necessary in connection with other variable features to summarise briefly the main facts regarding scale variations in Anophelines.

This is the more necessary in that it seems to be taken for granted that the only possible classification of the Anophelinae based on scales must be that actually employed by Theobald. That this is a very limited view to take must be granted by all who have paid close attention to scale characters. It may be found that other scale characters not perhaps so conspicuous as those so far employed may be of much greater use than has been suspected. It will be useful therefore, even if the subject is only rapidly passed in review, to indicate the broader principles of scale structure variation. In doing so I shall take the opportunity of making certain revisions in regard to the position certain species now occupy, positions which it would be unfair later on to consider as showing a discrepancy between the results of scale character and colour marking classifications.

Head Scales. Marked variations in the head scaling are restricted to a very few groups. The occurrence of linear head scales has been used by James[1] to differentiate the genus *Neostethopheles* (type *N. aitkeni*, James). This genus is clearly the same as Theobald's *Stethomyia* (type *S. nimba*, Theo.), in which the head scales are also linear. An examination of specimens of *A. corethroides*, Theo., in the British Museum shows that this unspotted winged species from Australia has linear head scales, and should come in the genus *Stethomyia* and not in *Anopheles* (vide also palpal characters). *A. immaculatus*, Theo., and *A. smithii*, Theo., have head scales of the ordinary expanding type.

Scaling of the palps. In some species the scales over most of the palps are of small size and relatively appressed. In such species the palp has a smooth thin appearance. In others the scales are long and outstanding, giving to the palp a more or less shaggy look. Difference in this respect, though not used in the definition of generic groups, is by no means unimportant. One would view with suspicion any supposed *Cellia* having smooth thin palps, or a supposed *Myzomyia* with shaggy palps. *Pm. rossi*, Giles, a species with shaggy palps until recently termed a *Myzomyia*, is now known not to conform in scale characters with the definition of this genus; presumably the related species *M. indefinata*, Ludlow, *M. ludlowi*, Theo., *M. mangyana*, Banks, are also rightly excluded. The species *M. lutzi*, Theo., at present the only South American representative of *Myzomyia*, has shaggy palps with a quite different type of ornamentation to that seen in any other *Myzomyia*, and the correctness of the present position of this species must be considered as problematical.

Between what may be called the *superpictus* group of *Pyretophorus*, which has very long thin palps, and *P. costalis*, Loew., there is also a very marked difference in this respect, which is accompanied by marked structural as well as important scale distinctions.

Antennal Scales. One of the characters of the genus *Calvertina* (*C. lineata*, Ludlow) is the presence of outstanding scales on the second segment of the antenna. I have not seen a specimen, but otherwise the scale characters from the description seem very like those of *Nyssorhynchus*. The markings also read very like those of *N. fuliginosus*, James and Liston.

Prothoracic Lobes. James (1) has called attention to the importance of the *patagia* or prothoracic lobes from the point of view of classification, and his separation of *Patagiamyia* (type *Pt. gigas*, Giles) from *Anopheles* is based on the presence in the former of a well-marked tuft of outstanding scales on these organs. Using this feature one can distinguish as *Patagiamyias*, in addition to those noted as belonging to the genus by James, *A. punctipennis*, Say., and *A. smithii*, Theo., both of which have prothoracic tufts.

Judging from the light thrown by colour markings, a tuft of scales on the prothorax is an extremely important character. Unfortunately it is only in a proportion of species that the description given notes the presence or absence of this character. A prothoracic tuft appears to be of general occurrence in *Myzorhynchus* (*barbirostris*, *umbrosus*, *sinensis*, *mauritianus*), there is a tuft in *Cycloleppteron grabhamii*, in *Arribalzagia maculipes* and in *Myzorhynchella nigra*. The tuft characteristic of *Patagiamyia* is present also in *Lophoschelomyia asiatica*, Leicester. *Myzorhynchus wellingtonianus*, Alcock, and *Feltinella pallidopalpi*, Theo., all of which species would appear from their colour markings to be related to *Pt. lindesayi*, Giles. A tuft is present in *Christophersia kochi* = (*Cellia kochi*, Donitz.), *Neomyzomyia elegans*, James, *Cellia squamosa*, Theo., and curiously enough in *P. costalis*, Loew. On the other hand, a large series of species do not show this structure.

At present, information is too scanty to enable any hard and fast use to be made of the prothoracic scaling in classification, but the table accompanying this section indicates approximately and very tentatively the possible significance of the occurrence of a tuft in this situation.

Mesothoracic Scaling. The presence or absence of broad scales on the thorax has been used along with other characters to differentiate a number of genera. Restricting observations to certain groups, the presence or absence of broad mesothoracic scales seems to serve the purpose of defining genera fairly well. By its aid *Myzomyia* is fairly clearly marked off from *Pyretophorus*, etc., and if the shape and character of the scales is also taken into account, this latter genus can be quite well differentiated from *Nyssorhynchus*.

Extending our observations, a good many reasons for restricting the significance of thoracic scaling become apparent, and any groups in which primary divisions were formed on this character would be very heterogeneous.

The great difficulty in scale structure is to know what significance can be attached to particular variations. Thus in comparing *Pm. ludlowi*, Theo., and *P. costalis*, Loew., which differ very slightly in markings, character of the palps, etc., one does not know whether the presence in the latter of mesothoracic scaling is to be taken as sufficient proof that they are unrelated or not. The same difficulty occurs in the case of abdominal scaling

Table shewing tentative grouping on general scale characters.

		Tuft on prothorax		No tuft on prothorax		
		Broad scales on mesothorax	No broad scales on mesothorax	No broad scales on mesothorax	Broad scales on mesothorax	
Head scales linear	Abdomen devoid of scales			Stethomyia (palps thin)		Wing scales moderately broad or narrow. Palps may be thin
Head scaling of ordinary type	Abdomen devoid of scales		Patagiamyia (Palps thin) Feltinella *My. natalensis*	Myzomyia Anopheles (Palps thin)	Pyretophorus (*nursei* group) (Palps thin)	
	Abdomen with a few scales on last segment, no tufts	*P. costalis* (wing scales not very broad)	Neomyzomyia	Pseudo-myzomyia		
	Scales on several segments, no tufts		Lophoschelomyia (Manguinosia) (?) (Kerteszia) (?)		Nyssorhynchus Neocellia	
	A ventral tuft often present with or without other scales		Myzorhynchus Cycloleppteron			Wing scales very broad. Palps shaggy
	Many ventral tufts	Christophersia				
	Lateral tufts	Arribalzagia (*C. mediopunctatus*) *C. squamosa*			Cellia (some species)	
Head scales appress'd	Abdomen without scales	Myzorhynchella				
Head scales narrow curved	Abdomen without scales	Chagasia				
Arrangement of scales peculiar	Abdomen with long lateral tufts		Christya (Peculiar genus narrow curved scales on prothorax)			

For most part wing scales very broad (Myzorhynchus-like) in the species *Ne. willmori*, James, and *N. maculatus*, Theo., which it is practically impossible or very difficult indeed to distinguish by any other characters than that one has a very much more scaly abdomen than the other.

Metathoracic Scaling. Limited observations only, which have not shown much promise, have been made in this respect. It was thought that since the metathorax represented a primary division of the thorax such scaling as was present might have more significance than its mere extent or conspicuousness might at first suggest.

The *halteres* which spring from the metathorax, as one might expect from their representing an undeveloped pair of wings, carry scales. Usually the halteres are quite ball like, but in certain species (e.g., *Arribalzagia maculipes*) the wing-like character is much more apparent (Plate VIII, fig. 39).

Wing Scales. Considerable differences occur in the shape of the wing scales. The most noticeable variation is in the breadth of the scales. There is also a difference pointed out by James, in that whilst in some species the scales are broadest in the middle (elliptical), in others they are broadest towards the free end (oblanceolate). This character serves, according to James, to distinguish between the genera *Anopheles* and *Myzomyia*.

Leg Scales. The genus *Lophoschelomyia* has been formed for *L. asiatica*, Leicester, which has outstanding scales on the femur. Recently another species showing the same appearance, *My. wellingtonianus*, Alcock, has been described. Examination of specimens in the British Museum shows that both these species are not only probably related to one another, but have affinities with *Pt. lindesayi*, Giles. *Pt. lindesayi* is at once differentiated by possessing a very striking white band about the middle of the femur. So far as one could see, this colour peculiarity was a pure idiosyncrasy of the species. But the presence of a white band in connection with the structural peculiarity of a prominent scale tuft on the femur in *L. asiatica* and *My. wellingtonianus* suggests that the band in *lindesayi* was once also accompanied by scale tufts. The band is not quite in the same position in *L. asiatica* as in *My. wellingtonianus* but its occurrence along with a scale tuft is unlikely to be a mere coincidence. The three species in question in any case appear to be closely related, and if the genus *Lopho-*

schelomyia is retained, it should probably include *Pt. lindesayi* (vide diagrams of wing markings, Pl. VIII, figs. 1, 3).

Abdominal Scales. Abdominal scaling, as pointed out by James, shows two distinct characters depending upon whether the scales project to form tufts or not.

Tufts are usually, but not always, associated with ordinary scaling. They may be lateral or ventral. The genus *Cellia*, as is well known, shows a marked development of *lateral tufts;* the same condition is shown in *Arribalzagia maculipes*, Theo. The peculiar species *Ch. kochi*, Donitz., shows a marked development of *ventral* tufts, whilst the (apparently) totally unrelated *Myzorhynchus* group has one such tuft (not, however, present in all species).

Pyretophorus is defined as having no scales on the abdomen. On close inspection I find that there are a few scales in *P. costalis*, Loew., especially in the male, the appearances being much like those seen in *Pm. rossi*, Giles. *P. costalis*, Loew., is the type of the genus, so that the definition of *Pyretophorus* (abdomen without scales) now held will not serve. The group of mosquitos like *P. nursei* seem to have a quite scaleless abdomen.

A common condition is that in which the last two or three segments only carry scales. This is best known in *Nyssorhynchus*, but it also occurs in *Lophoschelomyia*, *Manguinosia*, and *Kerteszia*.

In *Cellia*, *Neocellia*, *Christophersia*, and *Arribalzagia* the abdomen carries large numbers of scales.

In the table I give a quite tentative and provisional grouping based on scale structure, adopting as broad an outlook as possible. It will be noticed that I have given great prominence to the condition of the prothoracic lobes. It is possible that this may require modification, but at present all my observations have gone to show the extreme significance of the presence or absence of a tuft of scales on the prothorax.

VI. CLASSIFICATION, PHYLOGENY AND GEOGRAPHICAL DISTRIBUTION OF THE *ANOPHELINAE*

A tabular statement of groups as characterised, and to some extent defined, by structural characters and colour markings accompanies this paper. Though scale characters are given in this, they only enter very occasionally into the formation of the groups, and are purposely placed in parenthesis in order that their close agreement with the general scheme of classification given may be apparent. It will be seen that in the main Theobald's genera stand out clearly. Consideration of other characters, however, modifies Theobald's divisions as follows:—

(1) It shows certain genera to be composite.

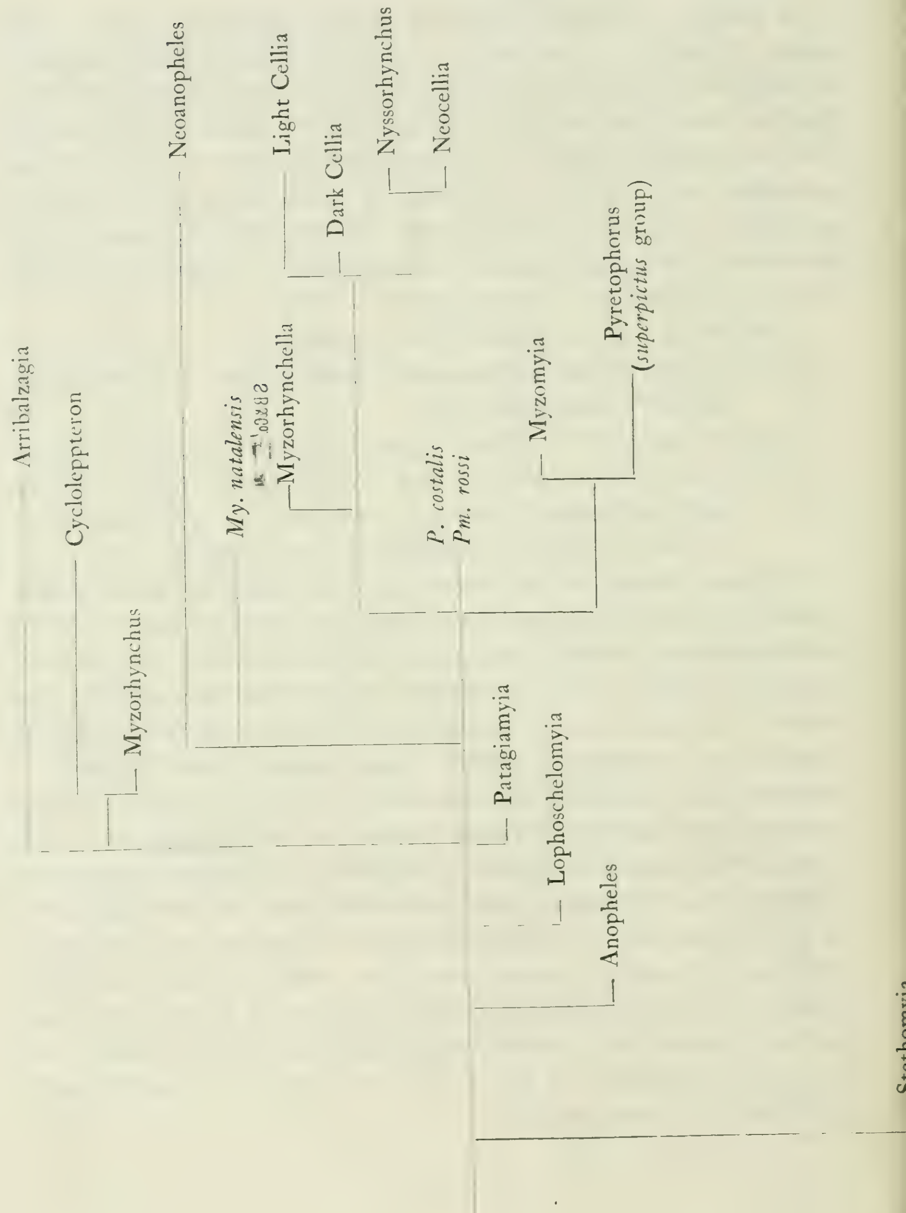
(2) It groups the genera together so that one has some realisation of their zoological value.

(3) It shows that it is not impossible that a system of quite good genera, more or less on Theobald's line, could be with advantage retained, and that it is premature to resort as yet to the abolition of this grouping.

I do not propose, in the present paper at least, to offer any new system of nomenclature, which would require, in order not to add to to the confusion already too apparent, the most careful and detailed systematic study of the subfamily. It will be sufficient for the present if the quite natural character of Theobald's genera, taken as a whole, is emphasized. What seems mostly now required is accurate and detailed descriptions of species, with a really comprehensive and authoritative revision of the Anophelinae. But a list of the groups as defined by structural characters and colour markings, and a tentative arrangement of these as they appear to be phylogenetically related, should not be open to any objection. Retaining Theobald's nomenclature, but noting the necessity of a number of emendations as regards the species at present contained in these genera, and subdividing the genera where necessary, the following represents, as far as one can judge, the phylogenetic relationship of these groups.

Towards elaboration of ornamentation and scale development

TENTATIVE PHYLOGENETIC ARRANGEMENT OF THE ANOPHELINAE



In this arrangement, phylogenetic advance is associated with both an increase in colour markings (i.e., the development of white) and in scaling. It is not difficult to arrange a correlation table in which increasing degrees of whitening and increased degrees of scaling form the ordinates and abscissae respectively. The striking nature of the correlation between the two series of characters is then made very apparent by the grouping of species about the diagonal line. The same correlation is also very evident in the phylogenetic scheme given.

Considering the fact that the Culicinae are all scaly, one might think it probable that Anophelines were a branch in which scales were disappearing. But my own observations on this point make it more probable that it is the other way. The more scaly an Anopheline is the more advanced phylogenetically it would appear to be.

Certain of the groups, it will be seen, occupy a much more primitive position in the scheme than others, and as this seems to be demonstrated by whatever character they are considered, and as there are definite characters by which one can distinguish these apparently old type species, I have named them *Protoanopheles*. The peculiar Australasian type I have called *Neoanopheles*. The ordinary Anophelines exhibiting the regular colour scheme I have outlined may approximately be termed the *Deuteroanopheles*. The nature of these groups, and the characters on which they are based, can be obtained from the large table accompanying this paper. Briefly stated, the constitution of the main groups noted is as follows:—

PROTOANOPHELES.

Stethomyia.
Anopheles.
Patagiamyia and *Lophoschelomyia.*
Myzorhynchus, *Cycloleppteron*, *Arribalzagia*, etc.

DEUTEROANOPHELES.

Myzomyia. *Pyretophorus.*	Branch A.
Pseudomyzomyia, etc.	Branch B.
Nyssorhynchus. *Neocellia.* *Cellia.*	Branch C.

NEOANOPHELES.

Many spotted winged species and their related types.

Between branches A and C of the Deuteroanopheles there are distinct differences in ornamentation, such as, for example, a much greater tendency to a completely broken third costal spot and narrow costal interruptions, but the most striking difference is in the much greater intensity of the black and white ornamentation. The origin of the branch B is difficult to determine. It is especially interesting as including some of the most dominant species, i.e., *Pm. rossi*, *P. costalis*, *Ne. stephensi*, *Pm. ludlowi*.

GEOGRAPHICAL DISTRIBUTION

Having on structural grounds arrived at certain groupings, it is interesting to note the geographical distribution of these groups.

Stethomyia, though it contains very few species, has a distribution area which includes South America and Australia, as well as India and Malay.

Myzorhynchus, if we consider the closely-related genus *Cycloleppteron*, also has a very extended distribution, which includes South America and Australia.

Anopheles and *Patagiamyia* are the dominant genera of Europe and North Amerca. There is, however, what appears to be an Australian representative of this branch, as well as hill species in the East.

In the case of the Deuteroanopheles, certain of the genera have a much more restricted distribution. Thus *Pyretophorus*, in the restricted sense in which I have been using the term, is dominant in Africa (North), occurs in South Europe and in the extreme North-west of India. It does not occur in South America or Australia, and it is scarcely represented in the Anopheline fauna of India and Malay.

Myzomyia is essentially African, Indian and Malayan.

Nyssorhynchus is also African and Malayan, with a distinct dominance in the latter area and in India.

The most widely distributed of the genera of the Deuteroanopheles is *Cellia*, and this fact is not out of keeping with the position assigned to this genus in the scheme of phylogeny.

The *Neoanopheles* are distinctly Australasian and Malayan.

More than the above outline of the main features of geographical distribution of species cannot be attempted here, but it will be seen that to a large degree consideration of the geographical distribution of species gives distinct support to the ideas respecting phylogeny which I have put forward in this paper.

VII. GENERAL CONCLUSIONS

Colour markings, equally with structural characters, can be utilised in natural classification of the Anophelinae and in the placing of species in groups to which they have affinities. A classification based on colour marking, supported by structural differences in the palps and larval characters, approximates very closely in regard to the groups formed with one based on scale structure. It shows, however, the relation and affinities between the groups much more clearly than does scale structure classification as at present employed in the distinction of genera.

Colour markings, and general characters as a whole, seem to point to there being a group of more primitive forms (PROTO-ANOPHELES) occurring as old world species (*Anopheles*, *Myzorhynchus* and *Patagiamyia*), and as new world representatives of this group *Cycloleppteron*, *Arribalzagia* and *Myzorhynchella*. There is also a distinct group corresponding to Donitz's Australasian species with more than three spots on the sixth vein (NEOANOPHELES). Their area of special prevalence is Australasia and Malaya.

The majority of Anophelines belong to a group the colour markings of which are all on a given colour scheme (DEUTERO-ANOPHELES). This group shows two main divisions, characterised by a notable difference in the intensity of their coloration and the 'effectiveness' of ornamentation, possibly arising from two different lines of evolution. Their area of special prevalence is an area including Africa, South Asia and Malay.

I am very greatly indebted to Prof. R. Newstead and to Mr. H. F. Carter for their great kindness in furnishing me with material for studying a number of African and South American species, including specimens of *Cy. grabhamii*, without which I could not have carried out many of my observations. I am also indebted to Prof. Newstead and Mr. Carter, as well as to Mr. F. W. Edwards, for their kindness in giving me every facility to make use of the collections at Liverpool and the British Museum respectively.

I also wish to acknowledge my indebtedness to Prof. G. H. F. Nuttall and to Mr. H. Scott, at Cambridge, for help in regard to literature and in other respects.

VIII. TABLE SHEWING GROUPING OF SPECIES OF ANOPHELINAE ACCORDING TO COLOUR MARKINGS AND OTHER VARIABLE CHARACTERS

A. NODAL CENTRES AT CROSS VEINS AND BIFURCATIONS DARK. (PROTOANOPHELES.)

A′. Costa devoid of any light areas even at apex. Wings usually without any pale markings.

1. Palps markedly heterodactylous with marked relative elongation of the second segment. Attitude *culex*-like. Wings entirely unspotted. Palps unbanded. Legs entirely without markings even knee spots being absent. Small mosquitos.

(Larval antenna without branched hair. Palmate leaflets lanceolate.)

Head scales linear. No scales on prothorax, mesothorax or abdomen.

Corresponds exactly with *Stethomyia*, Theo.; *Neostethopheles*. James.

S. nimba, Theo.

S. aitkeni, James and Liston.

S. culiciformis, James and Liston.

S. corethroides, Theo.

Probably synonyms—*S. treacheri*, Leicester; *S. fragilis*, Theo.; *S. pallida*, Ludlow.

2. Palps orthodactylous. Attitude *anopheles*-like. Palps thin, unbanded. Primitive spotting may be present. No admixture of light and dark scales. Knee spots usually present otherwise legs are quite unornamented.

(Larval antenna with branched hair (small), palm-leaflets lanceolate and serrated).

Head scales expanded. No prothoracic tuft. No scales on mesothorax or abdomen.

Corresponds with *Anopheles* sense of James.

A. maculipennis, Meigen.

A. bifurcatus, Linn.

A. nigripes, Staeger.

A. algeriensis, Theo.

A. barianensis, James.

A. barberi, Coq.

A. immaculatus, James. (?).

A. eiseni, Coq. (?).

A. crucians, Wied. (?).

A″. Costa with at least one pale interruption which may be at the apex.

(b′) Wings without prominent admixture of pale and dark scales.

3. Costa dark broken only at apex or at subcosta with or without small basal interruption. Palps usually unbanded. Primitive spotting prominent. Tarsus unbanded.

(Larva with branched hair on antenna. Palmate leaflets with filament but showing approach to lanceolate type.)

Head scales expanded. Tuft on prothorax. No broad scales on mesothorax. May or may not be scales on last segments of abdomen.

3*a*. With white band on femur which may be associated with tufts of outstanding scales in this situation.

Lophoschelomyia.
L. asiatica, Leicester.
L. lindesayi, Giles.
L. wellingtonianus, Alcock.

3*b*. Without white band or femur.
L. (?) *atratipes*, Skuse.

4. Costa prominently spotted. (Usually two, not more than three, main spots). Palps banded. Primitive spotting may be present (but not conspicuous). White spots on wings for most part represented on lower surface. Large mosquitos.

(Larval antenna carries a branched hair. Palmate leaflets with filament.)

Head scales expanded. Tuft on prothorax. No scales on mesothorax (or abdomen).

Corresponds to *Patagiamyia*, James.

Pt. gigas, Giles.
Pt. simlensis, James.
Pt. punctipennis, Say.
Pt. smithi, Theo. (Unspotted wings.)

Probably
A. formosus, Ludlow.

Perhaps
A. franciscanus, McCracken.
A. perplexans, Ludlow.
A. pseudopunctipennis, Theo.

Would probably include also
Feltinella pallidopalpi, Theo.

5. Costa dark with narrow interruptions but with four main costal spots. Wings markedly dark beneath. Palps shaggy.

(Larval antenna without branched hair. Palmate leaflets lanceolate.)

Head scales flattish. Broad scales on mesothorax. No scales on abdomen.

Myzorhynchella.

(*b''*) *Wings with prominent admixture of dark scales. Pale spots on the wing deficient as a rule on under surface. Hence, when third spot is light it shows dark border of projecting dark scales seen through wing membrane. Primitive spotting the rule. Sixth vein with at least one scale cluster of dark scales.*

(*Larval antennae with branched hair. Palmate leaflets lanceolate and serrated. Frontal hairs markedly branched.*)

Prothoracic lobes with tuft.

6. Legs not speckled. Costal edge dark with two (at most three) minute pale interruptions. Basal portion of costa unbroken by pale areas. Palps markedly orthodactylous, shaggy, unbanded or with scheme A ornamentation. Large mosquitos Old World species.

No broad scales on mesothorax. Some ordinary scales present or absent on abdomen. A ventral tuft of dark scales usually present on penultimate segment of abdomen.

Corresponds to *Myzorhynchus*.

My. barbirostris, Van der Wulp.
My. pseudobarbirostris, Ludlow.
My. bancroftii, Giles.
My. umbrosus, Theo.
My. strachani, Theo.
My. sinensis, Wied.
My. pseudopictus, Grassi.
My. paludis, Theo.
My. mauritianus, Grandpre.

7. Legs markedly speckled. Costal edge may be dark as in last group or broken into distinct spots. Accessory spot often present. Palps shaggy with scheme A ornamentation. Large mosquitos. New World species.

2*a*. Sixth vein with two dark spots. Wing with inflated scales but resembling that of Myzorhynchus in general arrangement.

No broad scales on mesothorax.

Cycloleppteron
Cycloleppteron grabhamii, Theo.

2*b*. Sixth vein with many spots.

Broad scales on mesothorax. Abdomen with many scales and lateral tufts.

Arribalzagia.
Ar. maculipes, Theo.
Cy. mediopunctatus, Theo.
(*Ar. pseudomaculipes*).
(*Ar. malefactor*).
(*Cy. intermedium*).

B. NODAL CENTRES AT CROSS VEINS AND BIFURCATIONS PALE. COSTA WITH FOUR DISTINCTLY MARKED MAIN COSTAL SPOTS.

B′. Palps Ornamented on Scheme A—C. Costa without Accessory Spots other than the basal ones. Not more than three dark spots on Sixth Longitudinal Vein. (DEUTEROANOPHELES.)

(*a*) Tips of hind tarsi not white.

a′. Palps markedly heterodactylous. Tips of hind tarsi never white. Banding of front tarsal joints never broad. Legs never markedly speckled. Wing markings of species on fixed scheme (Scheme A). If three spots are present on sixth vein there is a pale interruption on upper branch of second longitudinal. Completely broken third costal spot unusual.

(Larval antenna without branched hair. Palmate leaflets with filament. Frontal hairs usually simple unbranched.)

No prothoracic tuft. No scales on abdomen, even in male.

1. Sixth vein with two or less dark areas. No pale internodal spot on branch of fifth. Branches of second long, rarely with pale interruption. Still more rarely interruptions on branches of fourth. Fifth vein dark at junction of branch.

Mesothorax without broad scales.

Corresponds to *Myzomyia* in restricted sense (i.e., not including *Pm. rossi*, *M. lutzi*, etc.).

M. culicifacies, Giles.
M. nili, Theo.
M. rhodesiensis, Theo.
M. hebes, Donitz.
M. umbrosa, Theo.
M. listoni, Liston.
M. funesta, Giles.
P. sergentii, according to wing.

2. Sixth vein with three dark spots or two. Pale internodal spot on branch of fifth. Branches of two and four veins with pale interruptions. Fifth vein usually pale at junction of branch. Palps peculiarly long and thin. Not infrequently show apical dark band (four palpal bands) or apex dark.

Broad scales on Mesothorax.

Pyretophorus I (*superpictus* group).

P. superpictus, Grassi.
P. nursei, Theo.
P. nigrifasciatus, Theo.
P. cleopatrae, Willcocks (MSS.)
P. cardamatisi, Newstead and Carter.
P. distinctus, Newstead and Carter. Costa unusual but wing otherwise showing typical *Pyretophorus* condition.
P. palestinensis, Theo.
P. cinereus, Theo.

a''. Palps not markedly heterodactylous.

3. Upper branch of second vein with pale interruption.

Tip of hind tarsus not white. Palps destinctly orthodactylous but with whole of apical segment pale. Banding of front tarsus broad. Apical segment of palps in spite of length pale throughout. Hind tarsi not white but speckling usual. Whitening of wing considerable with completely broken third costal spot usual. All internodal pale spots developed and some residual pigment areas usually obliterated.

A composite group according to scale structure.

Prothoracic tuft. Preapical costal spot broken. Scales on mesothorax. A few scales on last segment of abdomen especially in male.

Pyretophorus II.

P. costalis, Loew.

(*P. pseudocostalis*, Theo. ?).

(*P. merus*, Donitz ?).

(*P. marshallii*, Theo. ?).

No prothoracic tuft. Preapical costal spot not broken. A few broad scales on mesothorax. A few scales on last abdominal segment especially in male.

Pseudomyzomyia, Theo. = *Nyssomyzomyia*, James.

Pm. rossi, Giles.

Pm. indefinata, Ludlow.

Pm. ludlowi, Theo.

No prothoracic tuft. Nyssorhynchus-like scales on thorax. *Ne. stephensi.*

4. Upper branch of second without pale interruption. Palps orthodactylous and with scheme A pattern. Bridging of pale spots on costa by dark areas on first long vein marked feature.

Prothoracic tuft. Broad scales on mesothorax. Abdomen with lateral tufts.

Cellia squamosa, Theo. Related to *Myzorhynchus* and Cellia. A peculiar species.

Isolated position in this table due to fact it does not possess white tips to tarsus. Note prothoracic tuft.

(*b*) Tips of hind tarsi white. Ornamentation very black and white. Speckling and banding usual. Full development of internodal pale areas of wing, but delayed appearance of pale area on upper branch of second vein.

(Larval antenna without branched hair. Palmate leaflets with filament. Frontal hairs often show some degree of branching.)

Characteristic broad white creamy scales on mesothorax.

5. Palps ordinarily three banded (scheme B). Orthodactylous or with some tendency in light forms to be slightly heterodactylous (*N. maculatus*).

Abdomen with scales on last few segments (*Nyssorhynchus*) or on many segments (*Neocellia*) but without lateral tufts. No prothoracic tuft.

Dark group. Upper branch of second long vein without interruption. Hind tarsi usually show uninterrupted white area extending over several segments. Palps destinctly orthodactylous, ornamented scheme B, with tendency in individuals to revert to A.

N. fuliginosus, Giles.
N. nivipes, Theo.
(*N. freerae*, Banks.)
(*N. phillipinensis*, Ludlow.)
Ne. fowleri, Christophers.
N. jamesi, Theo.
N. pretoriensis, Theo.
N. maculipalpis, James and Liston.

Light group. Upper branch of second long vein with interruption. Hind tarsi usually with alternate black and white areas. Palps with shorter terminal segment than last group and with scheme C ornamentation (two broad apical bands).

N. maculatus, Theo.
N. theobaldi, Giles.
Ne. willmori, James.

6. Palps ordinarily four banded (scheme A) and markedly orthodactylous.

Abdomen with lateral tufts. Prothoracic tuft in some species.

Cellia. Dark group. Bridging of pale spots on costa common. Also absence of interruption on upper branch second.

C. argyrotarsis, Desvoidy.
C. albimana, Wied.
C. jacobi, Hill and Haydon.
C. cincta, Newstead and Carter.
(*C. squamosa*, Theo. Hind legs not white, vide above.)
(*C. squamosa*, *var. arnoldi*. Hind legs not white, vide above.)

Light group. Upper branch of second interrupted. Costal spots not bridged.

C. pulcherrima, Theo.
C. pharoensis, Theo.

B″. Palps with Scheme D ornamentation. More than three dark spots on the Sixth Vein. Accessory costal spots often present in addition to basal ones. (NEOANOPHELES.)

With prothoracic tuft.

My. natalensis, Hill and Haydon. *
P. watsonii, Leicester. *
Nm. elegans, James. *
(*Nm. leucosphyrus*, Donitz.) *
N. annulipes, Walker. *
N. masteri, Skuse. *
Ch. kochi, Donitz.

Query any prothoracic tuft.

M. punctulata, Donitz. *
N. deceptor, Donitz. *
N. thorntonii, Ludlow.*
N. karwari, James and Liston.

All species show same character of palpal ornamentation.

* Shows more than three dark spots on sixth.

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EXPLANATION OF PLATES

Plate V

Fig. 1. Nymphal trumpets of *A. bifurcatus*, Linn.

Fig. 2. Nymphal trumpet of *Ne. willmori*, James.

Fig. 3. Leaflet of palmate hair of *My. sinensis*, Wied.

Fig. 4. Leaflets of palmate hairs. (*a*) *C. squamosa var. arnoldi*, after Newstead and Carter. (*b*) *N. annulipes*, Walker, after Theobald. (*c*) *A. bifurcatus*. (*d*) *Cycloleppteron grabhamii*, Theo., after Theobald. (*e*) *Myzorhynchus* (?) *natalensis*, Hill and Haydon, after these authors. (*f*) *P. ardensis*, Theo., after Hill and Haydon.

Fig. 5. Antenna of larva. (*a*) *A. bifurcatus*. (*b*) *A. punctipennis*, Say., after Smith.

Fig. 7. Female palp of *My. barbirostris*, Van der Wulp, showing orthodactylous character and unbanded condition.

Fig. 8. Female palp of *C. pulcherrima*, Theo. Orthodactylous with scheme A ornamentation.

Fig. 9. Female palp of *Pt. lindesayi*, Giles. Orthodactylous and unbanded.

Fig. 10. Female palp of *P. nursei*, Theo. Heterodactylous with appressed scales and scheme A ornamentation.

Fig. 11. Female palp of *P. jeyporensis*, James. Heterodactylous with appressed scales and ordinary Deuteroanopheles type of ornamentation, i.e., scheme B, with involvement of the whole of the apical segment.

Fig. 12. Female palp of *P. costalis*, Loew. Orthodactylous with scheme B ornamentation.

Fig. 13. Female palp of *M. funesta*, Giles. Heterodactylous with appressed scales and scheme B ornamentation.

Fig. 14. Female palp of *N. maculatus*, Theo. Scheme C ornamentation.

Fig. 15. Female palp of *N. maculatus* contrasted with palps ornamented on scheme D. (*a*) *N. maculatus*. (*b*) *M. punctulata*, Donitz. (*c*) *Ch. kochi*, Donitz. (*d*) *N. karwari*, James. After James.

Fig. 16. Sketch of palp of *S. corethroides*, Theo., showing remarkable modification in the relative lengths of the different segments. Heterodactylous. Type 2.

Fig. 17. Palp of *S. nimba*, Theo., after Theobald.

Plate VI

Fig. 1. Diagram showing structural features of wing and leucogenetic centres. Nodal points are shown by small circles, internodal by larger ones. Pigment centres are shown dark.

Pigment centres.

Ac′., *Ac″.* Basal accessory pigment areas.

i.m.c. Inner main costal spot centre.

m.m.c. Middle main costal spot centre.

s.a.m.c. Subapical main costal spot centre.

a.m.c. Apical main costal spot centre.

2*r.*, 2*a.* Basal and apical centres of stem of second vein.

2′*b.*, 2′*a.* Inner and outer centres of upper branch of second longitudinal vein.

2″*a.*, 2″*b.*, 2″*c.* Outer, inner and middle centres of lower branch of second vein.

3*a.*, 3*b.* Residual pigment centres of third longitudinal.

4*r.*, 4*a.* Centres on stem of fourth longitudinal.

4′*a.*, 4′*b.*, 4″*a.*, 4″*b.* Centres on fork of fourth longitudinal.

5′*a.*, 5′*b.*, 5′*c.* Centres on branch of fifth longitudinal.

5*r.*, 5″*a.* Characteristic centres of fifth longitudinal vein.

6*r*, 6*m*, 6*a*. Centres for sixth vein. 6*r.* is Donitz's root spot of sixth.

Nodal points.

h. Humeral.

Sc. Subcostal.

Ap. Apical.

S. Sector.

S′. Accessory sector.

C_1, C_2, C_3, C_4, C_5. Nodal points in connection with cross veins.

*C.*1′. (?) Nodal point concerned in the formation of the inner pale spot on costa.

*C.*1″. (?) Nodal point concerned with subapical spot.

1, 2′, 2″, 3, 4′, 4″, 5′, 5″, 6. Nodal points on wing margin.

Internodal points.

2^1, 2^2, 2^3. Internodal points on branches of second vein. The relatively late appearance of 2^1 is characteristic of *Nyssorhynchus* and dark *Cellias*.

3, 3. One or two internodal points of third vein.

4, 4^1, 4^2. Internodal points of stem and branches of fourth vein.

5^1, 5^2, 5^3. Points on main vein and branch of fifth vein.

6^1, 6^2. Points on sixth vein.

Fig. 2. Portion of the wing of a species of *tipulidae*, showing venation homologies and extra cross veins.

h. Humeral cross vein.

C.1′. Cross vein joining subcosta to first longitudinal.

C.1″. Ditto upper branch of second to first longitudinal.

R_1, R_2, R_3, R_{4+5}, Radial system.

R.S. Radio-sector.

S. As in figure 1.

S′. Ditto.

Fig. 3. Showing area of cross veins, and relation to nodal point *S*.

Cv_2, Cv_3, Cv_4, Cv_5. Cross veins 2-5.

S. = Sector, *S*′. = Accessory sector nodal point.

sc. = Subcosta.

Fig. 4. Wing of a species of *Chironomus*, showing pale spots on wing membrane involving the hair-like scales covering the wing and aggregation of hair-like scales to form dark spots at the area of the cross veins.

Fig. 5 to Fig. 13. Diagrams of representative wings, showing arrangement of nodal and internodal points as developed in different groups.

Dark spots represent nodal points which remain pigment areas. Circles half dark represent pale spots not developed on under surface of the wing. Small black dots in circles mean admixture of dark and light scales present. Dark stars mean scale aggregations.

PLATE VII

Fig. 1. Wing of *A. maculipennis*, showing primitive spotting.

Fig. 2. Wing of *My. umbrosus*, showing primitive spotting, want of representation of pale spots on under surface of wing, and admixture of dark and light scales. A scale cluster on the sixth vein is also shown.
2a. Under surface.

Fig. 3. Wing of *M. funesta var.*, showing first appearance of nodal points with few internodal centres. Pale scaling not intensely white.

Fig. 4. Wing of *N. maculatus*, showing extreme development of nodal and internodal centres, with residual pigment areas well displayed. White scaling intensely white.

Plate VIII

Diagrams of the spotting of the wings in a number of species of Anophelinae, especially to show arrangement of costal spots. Figs. 1-38.

Fig. 39. Halter of *Cy. mediopunctata*, showing resemblance to unexpanded wing, with light scaling above and intensely dark scaling beneath.

1. *Patagiamyia lindesayi*, Giles.
2. *My. wellingtonianus*, Alcock.
3. *Lophoschelomyia asiatica*, Leicester.
4. *Patagiamyia gigas*, Giles.
5. *Patagiamyia simlensis*, James, *var.*
6. *Myzorhynchus umbrosus*, Theo.
7. Ditto under surface.
8. *Myzorhynchus mauritianus*, Grandpré.
9. *Myzorhynchus sinensis*, Wied.
10. *Cycloleppteron grabhamii*, Theo.
11. Ditto under surface.
12. *Cycloleppteron mediopunctatus*, Theo.
13. *Arribalzagia maculipes*, Theo.
14. *Myzorhynchella nigra*, Theo.
15. Ditto under surface.
16. *Cellia squamosa*, Theo.
17. *Cellia squamosa*, Theo.
18. *Nyssorhynchus fuliginosus*, Giles.
19. *Myzorhynchus* (?) *natalensis*, Hill and Haydon.
20. *Pyretophorus* (?) *watsonii*, Leicester.
21. *Neomyzomyia leucosphyrus*, Dönitz.
22. *Myzomyia* (?) *punctulata*, Dönitz.
23. *Christophersia kochi*, Dönitz.
24. *Nyssorhynchus* (?) *annulipes*, Walk. (Costa only shown.)
25. *Pyretophorus costalis*, Loew.
26. *Cellia jacobi*, Hill and Haydon.
27. *Myzomyia culicifacies*, Giles.
28. *Myzomyia listoni*, Liston.
29. *Pyretophorus cinereus*, Theo.
30. *Pyretophorus nursei*, Theo.
31. *Pyretophorus cardamitisi*, Newstead and Carter.
32. *Pyretophorus chaudoyei*, Theo.
33. *Pyretophorus jeyporensis*, James.
34. *Nyssorhynchus theobaldi*, Giles.
35. *Neocellia stephensi*, Liston.
36. *Pseudomyzomyia rossi*, Giles.
37. *Pyretophorus ardensis*, Theo.
38. *Pyretophorus* (?) *atratipes*, Skuse.

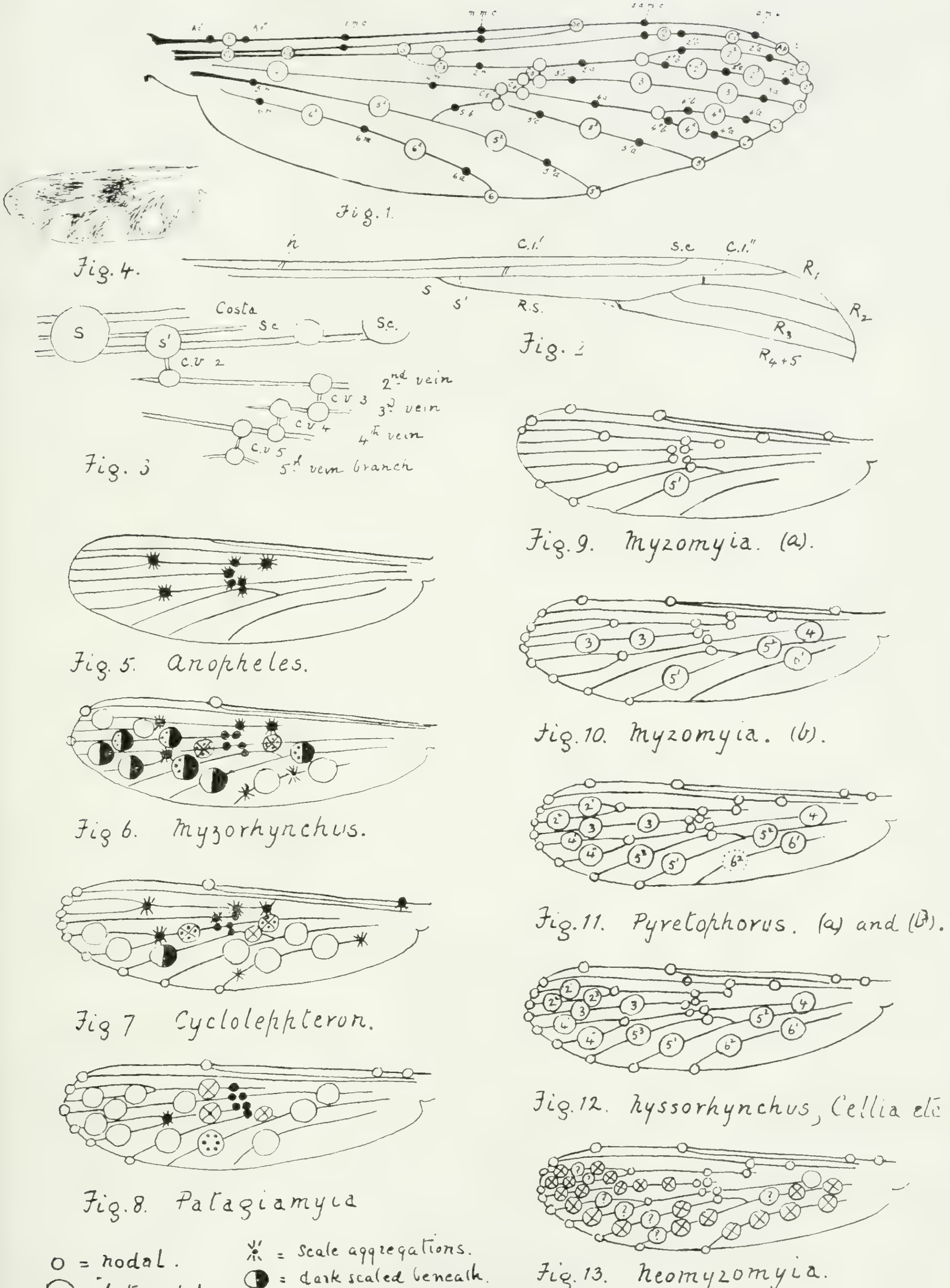

Fig. 1.

Fig. 2

Fig. 3

Fig. 4.

Fig. 5. Anopheles.

Fig 6. Myzorhynchus.

Fig 7 Cyclolepteron.

Fig. 8. Palagiamyia

Fig. 9. Myzomyia. (a).

Fig. 10. Myzomyia. (b).

Fig. 11. Pyretophorus. (a) and (b).

Fig. 12. Nyssorhynchus, Cellia etc

Fig. 13. Neomyzomyia.

o = nodal.
◯ = Internodal
⊗ = additional
✳ = Scale aggregations.
◐ = dark scaled beneath.
⊙ = mixed dark and light scales

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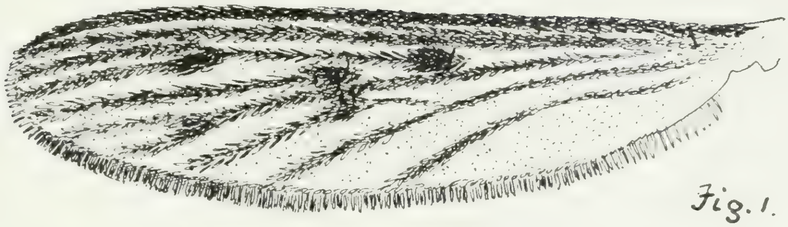

Fig. 1.

Fig. 2

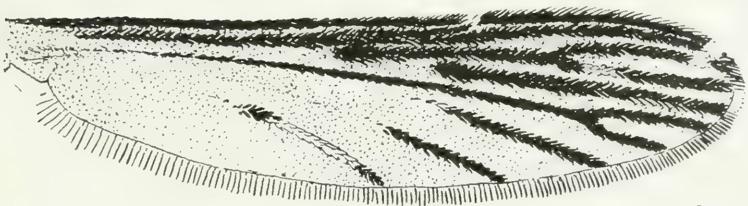

Fig. 2.a.

Fig. 3.

Fig. 4.

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